Art. VIII.—*Preliminary Notes on the Structure and Development of a Horny Sponge* (*Stelospongus flabelliformis*).

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I.—Anatomy and Histology.

(*a*) *External Characters.*—This sponge, which was discovered by Mr. J. Bracebridge Wilson, M.A., near Port Phillip Heads, Victoria, and briefly described by Mr. H. J. Carter in the Annals and Magazine of Natural History, consists of a stout cylindrical stalk terminating below in a basal expansion for attachment to the substratum and above in a broad, compressed, but thick frond. Along the upper margin of the frond is a single row of large oscula. The character of the surface of the frond is subject to considerable variations. On both sides it usually exhibits a number of prominent, branching and anastomosing ridges, enclosing a number of concave depressions. The entire surface of the sponge is more or less thickly encrusted with particles of sand; these are, however, more abundant over the ridges than in the depressions, and the latter are characterised by a minutely reticulate appearance, due to the presence of the inhalant pore-areas. The pores are enormously abundant all over the depressed portions of the surface, but are absent on the ridges.

(*b*) *Skeleton.*—The skeleton is composed of a rather irregular reticulation of cylindrical horny fibres, branching and anastomosing freely. The fibres are rather slender and the meshes between them are wide. It is easy to distinguish primary and secondary fibres. The primaries are long and rather stouter than the secondaries, about 0·096 mm. in diameter. They radiate towards the surface of the sponge, and end in the sandy incrustation. They are easily distinguished by the presence in them of numerous foreign bodies, which form an axial core, surrounded and held together by the spongin. The secondary fibres are short and contain no foreign bodies, they run in various planes and unite together adjacent primary fibres, meeting them at various angles; they may also branch and anastomose *inter se*.

Thus the skeleton is thoroughly typical in structure and arrangement, and essentially the same as that of the ordinary bath sponge, only much coarser.

In the stalk, the skeleton is more strongly developed, and hence the latter acquires a tougher and denser character than the remainder of the sponge.

(*c*) *Canal System.*—The inhalant apertures, or pores, are thickly scattered all over the depressed areas on the surface of the sponge. These larger areas are themselves subdivided into a great number of smaller ones, which are the true pore-areas, comparable to the pore-sieves of *Phakellia* and *Myxilla*. Each pore-area is irregularly rounded or oval in outline, and measures about 0·19 mm. in its longer diameter. Each one overlies a subdermal cavity, and contains five or six oval or rounded pores, averaging 0·05 mm. in diameter.

The subdermal cavities are hollow spaces in the ectosome, corresponding in size and shape to the pore-areas which they underlie, and communicating with the exterior by means of the pores in the latter. Adjacent subdermal cavities are separated from one another by anastomosing vertical walls of tissue, constituting the bulk of the ectosome, and each communicates below with an inhalant space or canal. Thus each subdermal cavity receives the water from the exterior through five or six distinct apertures (the pores) in its roof, and passes it on through a single (?) aperture in its floor into a large inhalant channel. Just as a number of pores lead into one and the same subdermal cavity, so also a number of subdermal cavities lead into one and the same inhalant channel. There is, however, a good deal of variation in the arrangement of the inhalant canal system, and it would probably be difficult to find two cases in which it was exactly alike. The large inhalant channels, into which the subdermal cavities directly open, lead, in their turn, into an irregular system of much smaller, more or less lacunar channels, whose ultimate ramifications open into the flagellated chambers.

Numerous flagellated chambers open out of one and the same ultimate inhalant lacuna. The chambers themselves are more or less spherical sacs, about 0·04 mm. in diameter, with two wide apertures of about equal size placed at opposite poles, whereby they communicate on the one hand with an ultimate inhalant lacuna, and on the other with an ultimate exhalant lacuna. Several chambers may lead into one and the same ultimate exhalant lacuna.

Both the inhalant and exhalant apertures of the flagellated chambers are usually drawn out into short and relatively wide cameral canaliculi, much as in *Euspongia officinalis*, as figured by Schulze.

The exhalant canal system is partly lacunar and partly composed of very definite tubular canals (the oscular tubes) with proper walls of their own, separable from the remainder of the choanosome. The ultimate exhalant lacunæ, into which the flagellated chambers open, collect together and finally discharge their contents into branches of the oscular tubes. Each oscular tube is a perfectly definite, wide, cylindrical canal, with distinct walls, and leads vertically upwards to a wide circular osculum situated on the upper margin of the sponge.

In connection with the exhalant canal system, I must also mention certain spherical cavities lying in the neighbourhood of the oscular tubes, and containing each a single large embryo. These cavities appear now to be entirely closed and cut off from the remainder of the canal system of the sponge, but it is possible that they are really portions of the exhalant canal system, specially modified to serve as receptacles in which the embryos are lodged during a large portion of their development.

(*d*) *Histology of the Soft Tissues.*

A. *The Ectosome.*—The ectosome forms an external layer of varying thickness all over the surface of the sponge. Owing to the presence in it of a large amount of sand, especially abundant on the raised ridges, it is very hard and tough, and forms an excellent protection against the attacks of parasitic crustaceans, worms, &c., to which sponges are very subject.

The outermost layer of the ectosome is formed by an extremely thin and delicate epidermis, most readily visible in the pore-areas, where the sand grains are absent. The nuclei of the epidermic cells may be easily distinguished in the transparent pore-bearing membrane; they are round or oval in shape, and about 0·0048 mm. in diameter.

Beneath the epidermis a very large proportion of the ectosome is occupied by the sand grains above mentioned, but surrounding these is a considerable quantity of mesodermal tissue. This is for the most part made up of cystenchyme, but stellate mesoderm cells are also present.

The name *Cystenchyme* has been applied by Sollas to a peculiar form of tissue not uncommonly met with in the ectosome of sponges. In *Stelospongus*, the cystenchyme cells are oval or subglobular in shape, measuring about 0·024 mm. in diameter, and the nucleus is small and granular. The protoplasmic strands which connect the nucleus to the cell wall are best seen in unstained preparations mounted in glycerine. They are then seen to form a network, branching and anastomosing *inter se*. In balsam preparations, owing doubtless to the greater transparency, the protoplasmic strands are not nearly so distinct.

I may mention here that cystenchyme occurs also in the choanosome of *Stelospongus*, but to this point I shall return later on.

The stellate mesoderm cells of the ectosome appear to be thoroughly typical. They may be seen investing the grains of sand in a kind of delicate network, the individual cells being mutually connected by long delicate processes. The body of the cell is somewhat granular, and the nucleus is oval and of moderate size.

(B.) *The Choanosome.*

(1) The walls of the inhalant and exhalant canal system.—It will be convenient to give these the first consideration because of their close relationship to the ectosome, from which they cannot be sharply separated.

The larger or proximal portions of the inhalant canal system are provided with special walls of mesodermal tissue. The true nature of this lining membrane is difficult to determine. In sections it is seen to consist of a very much vacuolated, gelatinous substance, composed more or less of cystenchyme, but in parts becoming fibrous.

The ultimate inhalant lacunæ have no special mesodermal walls, but here the nuclei of a lining epithelium can be easily detected in thin sections.

The ultimate exhalant lacunæ also have no special mesodermal walls, but are lined by a delicate flattened epithelium. The larger exhalant canals, or oscular tubes, are, however, provided with most distinct walls, which can be dissected out from the underlying tissues with great ease. These walls are membranous and fairly tough, and they are continued from the oscular tube along its various larger branches as a distinct lining membrane.

The wall of the oscular tube is seen in transverse section to be made up of the following layers, from within outwards ; (*a*) Furthest from the lumen of the tube, a thick, rather irregular layer of very much vacuolated, gelatinous tissue ; (*b*) A much thinner layer of deeply staining, fibrous tissue, in which the fibres are closely packed and arranged circularly around the oscular tube. (*c*) A continuous layer, only about one cell thick, of cystenchyme.

I have no doubt that the wall of the oscular tube is completed on the inside by a delicate, flattened epithelium, but I have not succeeded in demonstrating its presence.

(2) The walls of the embryo-containing cavities.—Whatever view may be adopted as to the relationship of the embryo-containing cavities to the exhalant canal system, it will be convenient to describe the structure of their walls in this place.

The only ovum which I have observed, previous to the commencement of segmentation, lies in a small cavity about 0·1 mm. in diameter, situate in the innermost part of the gelatinous layer of the wall of an oscular tube. This cavity has a special wall composed of fibrous tissue, with elongated nuclei. I have not detected any lining epithelium, although some of the nuclei observable may possibly belong to a delicate epithelial layer.

The large embryo-containing capsules are doubtless developed by growth of the small ovum-containing capsules. The walls of the large capsules are, however, very much more highly developed, and consist of two very distinct layers :—(*a*) A fibrous layer, and (*b*) a lining epithelium. The fibrous layer is very dense next to the lining epithelium, but further in it becomes looser, and is broken into by large lacunar spaces. It is composed of circularly arranged fibres, each consisting of a greatly elongated, fusiform, granular cell, with a deeply-staining, oval nucleus in the centre. The fibres are so densely packed in the outer part of the layer, next to the lining epithelium, that the outlines of the individual cells can no longer be distinguished ; but further in the cells lie further apart, and the tissue partakes more of the nature of a compact, stellate mesoderm.

The lining epithelium of the embryo capsule is very peculiar, and, so far as I am aware, entirely different from anything which has hitherto been described in sponges. It is composed of a single layer of enormous polygonal cells. These cells, although flattened, are thick. In the youngest embryo capsule they average about 0·072 mm. in diameter, but up to 0·12 mm. in diameter in older ones, and they are about 0·024 mm. in thickness. The body of the cell is finely granular, and each contains in its centre a very large, flattened, oval nucleus, enclosing a number of deeply staining granules. In transverse sections, the outer surfaces of the cells are very often seen to be indented, and these indentations would appear to correspond in some way to the upper portions of the outer layer of cells of the embryo, which in life are closely connected with the epithelial layer of the embryo capsule. In transverse sections also the body of the cell is seen to be granular throughout, but the granules are very much finer around the nucleus than towards the periphery of the cell. The cell always has a very definite bounding wall on its outer and sometimes also on its inner surface; but frequently its inner surface, which in life is pressed against the fibrous layer of the embryo-capsule, exhibits no such wall. In sections the nucleus sometimes appears solid and sometimes as a hollow vesicle provided with a distinct wall and enclosing a granular substance.

These large epithelial cells very readily become detached from the underlying fibrous layer of the capsule, and sometimes remain adherent to the embryo when the latter is removed from the mother sponge.

Owing to its relationships to and intimate connection with the outer layer of cells of the embryo, and for certain other reasons, I believe this peculiar lining epithelium of the embryo capsule to be nutritive in function.

(3) The walls of the flagellated chambers.—The walls ot the flagellated chambers are, of course, composed of collared cells, but these cells exhibit certain very interesting details in structure.

Last year Professor Sollas showed* that in certain sponges the collars of the collared cells (*choanocytes*) are united together at their margins by a continuous membrane, which forms a kind of inner lining to the chamber. I have

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* Article Sponges in the Encyclopædia Britannica. Ed. ix.

been able to demonstrate the existence of this connecting membrane, which for the sake of convenience we may term Sollas's membrane, in the flagellated chambers of *Stelospongus.*

The collared cells are arranged at about equal distances all around the chamber, but they are interrupted at the proximal pole by the inhalant aperture, and at the distal pole by the exhalant aperture. They are not all of the same size, but largest around the inhalant aperture, and gradually diminishing towards the exhalant aperture, around which they are smallest. Each cell consists of a cylindrical collum or neck with a large nucleus lying in its slightly expanded base (the body of the cell). The collum projects into the chamber, and gives support to the delicate membranous collar, which is rather longer than the collum, and considerably wider at its summit. Thus the whole cell, including the collar, has somewhat the shape of a dice-box, being narrower in the middle than at the two ends. I have not been able to trace any definite outline to the body of the cell, which is imbedded in a highly granular ground substance, but the nuclei are always very conspicuous. The flagella cannot be detected in my preparations, being entirely shrivelled up, or possibly retracted when the sponge was placed in spirit.

The margins of the collars are all connected together by a continuous delicate membrane (Sollas's membrane), which lies in a plane at right angles to the long axis of the collared cell. This membrane is seen in thin vertical sections as a fine thread running from collar to collar. If, however, the sections be taken in a plane more or less parallel to Sollas's membrane, then the latter frequently appears as an irregular network of delicate transparent strands, shrivelled up and distorted by the action of reagents, but easily recognisable lying within the chamber.

From what has been said of the sizes and arrangement of the collared cells in each chamber, it will be seen that the membrane joining their margins will not run parallel to the wall of the chamber, but will be furthest from it at the proximal or inhalant pole, and nearest to it at the distal or exhalant pole. At the proximal pole, in fact, the membrane is widely separated from the wall of the chamber, while at the distal pole, the two became confluent. Hence the membrane has the form of a cup, whose concavity is turned towards the exhalant aperture of the chamber.

(4) The general mass of mesodermal tissue in which the canals, flagellated chambers and other structures are imbedded.—

The flagellated chambers are pretty closely packed together in the choanosome, and together with the various branches of the canal system, make up the greater part of its bulk. Hence the amount of fundamental or ground tissue in which they are imbedded is not very great. What there is is packed full of minute, highly refringent granules, fairly evenly distributed through it. Imbedded in this granular matrix may be observed, here and there, small nucleated cells of irregularly rounded outline, doubtless the amœboid cells of authors. This ground tissue appears to agree thoroughly with that which Schulze has described as existing in Euspongia.

(5) The spongoblasts and other mesodermal cells surrounding the fibres.—

In most parts the skeleton fibres are surrounded by a sheath of ordinary stellate or slightly fibrous connective tissue. In some places, however, the stellate mesoderm cells are specially modified as *spongoblasts* or glandular cells whose function it is to secrete the spongin of which the horny fibre is composed. The spongoblasts form a layer one cell thick around the fibre. Each one is a somewhat club-shaped, slender, elongated, granular mesodermal cell, about 0·048 mm. long; one end is drawn out into a long, gradually tapering neck, and the other, broader end is usually rounded off, but sometimes stellate, and contains a spherical nucleus. The whole cell is frequently more or less bent or contorted. Its long axis, however, always lies approximately at right angles to the surface of the fibre against which its narrow end abuts. There is commonly, if not always, a layer of stellate mesoderm outside the layer of spongoblasts, and it is easy to see that the spongoblasts themselves are simply slight modifications of the ordinary stellate type of cell.

II.—Development.

My observations on the embryology of *Stelospongus* are as yet very imperfect, for all the embryos which I have as yet found are in pretty much the same stage of development. Of this particular stage there is, however, an abundant supply, and it presents some very remarkable features.

The ovum, of which I have found one example in my sections, appears in section as a somewhat oval cell, lying in a fibrous capsule, as described above. The body of the ovum is granular and deeply staining. At one pole there is a large, oval nucleus, with a very definite wall, and right up against the wall at the outer pole of the nucleus there lies a small, spherical nucleolus. Within the nucleus there is a quantity of coarsely granular protoplasm, chiefly aggregated towards the pole remote from the nucleolus. The nucleolus stains deeply and is almost if not quite homogeneous.

The embryos, which are abundant, are spherical solid bodies, about as large as small peas. When the surface of the embryo is examined with a pocket lens, it exhibits a minutely punctate appearance, due to the presence of an immense number of shallow pits, somewhat polygonal in outline and separated from one another by low ridges. Each one of these pits is the imprint of one of the large epithelial cells of the embryo capsule.

In sections, the embryo is seen to consist of an outer layer of rather large, closely packed cells, enclosing a central mass of clear, transparent, jelly-like substance, in which immense numbers of amœboid wandering cells are imbedded. The outer layer, or ectoderm, consists of a single layer of large, sac-shaped or somewhat flask-shaped cells, measuring about 0·024 mm. in length. The narrower portion, or neck of the cell is on the outside of the embryo, and the swollen portion projects inwards into the gelatinous intercellular substance, and from its inner extremity the cell frequently sends out a few short, slender, protoplasmic processes, resembling pseudopodia. The body of the cell is coarsely granular, but less so in the neck than in the swollen portion. The greater part of the neck is, however, occupied by a large, spherical nucleus, which appears to consist of a hollow vesicle containing a few deeply staining granules. The nuclei of adjacent cells are all arranged at just about the same level, so that they form a continuous row, which is a very conspicuous feature in transverse sections of the embryo.

Frequently the outer end of the neck of each ectodermal cell may be seen to be drawn out into a short, slender protoplasmic process, which extends to the outer surface of one of the large, investing epithelial cells and attaches itself to it. Thus the ectodermal cells of the embryo often appear to be suspended from the outer surfaces of the investing epithelial cells by short protoplasmic processes. Judging from the number seen in a single transverse section, it would appear that each of the large epithelial cells may have a hundred or more sac-shaped ectodermal embryonic cells hanging from its lower surface.

The unusual length of time during which the embryo remains within the mother sponge, and the great size to which it attains, necessitate some special arrangement whereby it can be nourished. The peculiar relations of the ectodermal cells of the embryo to the investing epithelium, and the very unusual character of the latter, cause me to believe that the investing epithelium has for its function the nutrition of the embryo, and that this is effected by the absorption of nutriment through the necks of the ectodermal cells.

Sometimes, however, the ectodermal cells exhibit no prolongations of the neck, but are smoothly rounded off at the free end, and such cells may form a continuous layer over a considerable area.

The entire mass of the embryo, within the ectodermal layer, is made up of a clear, jelly-like matrix, in which immense numbers of large, amœboid wandering cells are imbedded. These cells appear somewhat larger than the ectodermal cells, but there is very strong reason for believing that they are simply ectodermal cells which have left their place in the outer layer and, becoming amœboid, wandered into the central jelly. Between the large amœboid cells very delicate branching stellate cells may sometimes be seen. The amœboid cells may put out pseudopodia in all directions, but often they appear to be radially elongated, and more or less bi-polar. I think my sections show conclusively that the amœboid cells are derived from the ectodermal layer. They agree at first in all essentials with the cells of the latter, and in those parts where the ectodermal cells have the clearer, outer end of the neck evenly rounded off—and thus present a characteristic feature—a precisely similar clear rounded neck may often be seen in the cells immediately beneath the ectoderm.

The amœboid cells are from the first highly granular, and at what I believe to be an early stage in the proceedings each one has a spherical nucleus, resembling that which occurs in the ectodermal cells. Sometimes the amœboid cells lying near the outside of the embryo have two or three nuclei, and very rarely also even the ectodermal cells appear to have two nuclei. At a later stage, the entire cell is seen to have become indistinct in outline, and in place of one large cell we have an aggregation of very many minute spherical bodies, each with a dark spot in its centre, but each aggregation still retains the form of the original amœboid cell. In the same sections which exhibit this condition many of the amœboid cells appear to have become rounded off, and their contents have arranged themselves around a central cavity, so that we have a hollow chamber lined by small spherical cells. These chambers I believe to be the young flagellated chambers. They are certainly very different in structure from the flagellated chambers of the adult sponge, and only about half the size; but this difference is readily explained by their embryonic condition. I have not been able to trace the development of the chambers any further, nor is it to be expected that the collars and flagella would be developed before the young sponge was set free and required them.

Coincidently with the formation of the chambers in the manner just described, a slit-like invagination appears on the surface of the young sponge, and it is chiefly, if not solely, around this invagination that chamber formation takes place. This invagination I believe to be the commencement of a communication between the chambers and the outside. Unfortunately, I have only obtained a single embryo which is sufficiently advanced to show the formation of the flagellated chambers and the slit-like invagination, but I see no good reason for doubting the normality of the phenomena above described.

It thus appears that the flagellated chambers in *Stelospongus* are formed by the breaking up of large amœboid cells, exactly as described by Mr. Carter in the development of the gemmules of *Spongilla*.